

How is the invasive gorse *Ulex europaeus* pollinated during winter? A lesson from its native range

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Abstract Many examples of plant-insect interactions have shown that selection from herbivores can act on flowering and fruiting phenology. In *Ulex europaeus* (Fabaceae), escaping seed predation resulted in extended, but variable flowering periods, with some plants flowering from autumn until spring and others flowering only in spring. The present study aims at understanding how gorses can have a high reproductive success during winter despite harsh climatic conditions and low number of pollinators. We measured pollen production, flower size and seed production in spring and winter, and compared the different seasons. The pollination success of flowers was high in both seasons. The flowers produced as much pollen, and were of comparable size in spring and winter, but they stayed open twice as long in winter than in spring. The high pollination rate we observed was thus due to the longer opening period of flowers and the high attractiveness of flowers during winter. However, pod abortion was higher in winter, with 43% of the flowers in winter and 75% in spring

producing ripe pods. Antagonistic selective pressures exerted by biotic and abiotic interactions may, therefore, have lead to the observed flowering polymorphism, and allow *U. europaeus* to thrive in various climates, thus, increasing its invasiveness in different countries.

Keywords Flowering phenology ·
Invasive plant · Pollination · Seed predation

Introduction

Flowering and fruiting phenology can strongly influence reproductive success (Rathcke and Lacey 1985) and as such, should show some trends towards optimal timing and duration. Although it has been argued that selection is more likely to act on traits other than phenology (Ollerton and Lack 1992), changes in phenology do occur, and several causes and mechanisms can be involved (LeBuhn 1997). Phylogenetic constraints have been invoked to explain specific patterns of flowering phenology (Kochmer and Handel 1986), but exceptions are found where phylogeny does not explain the phenology observed (SanMartin-Gajardo and Morellato 2003). Both abiotic and biotic environments can select for changes in flowering and fruiting phenology (Brody 1997; Elzinga et al. 2007). Often, herbivores and pollinators are mentioned as imposing a strong pressure on plant traits within genera

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(Crawley 1989), and both of them can affect plant phenology (Brody 1997). In fact, selection pressures from herbivores and pollinators can counterbalance one another when the same cues attract both pollinators and seed predators (Zimmerman 1980). The complexity of these many influences operating on a species phenology implies that it is not sufficient to examine phenology in isolation (LeBuhn 1997), and that its study should be rather integrative.

Regarding phenology, the case of *Ulex europaeus* (Fabaceae, Genisteae) is very peculiar. Indeed, its phenology of flowering and fruiting is unusual: in its native range (South-Western Europe), its main flowering period is spring, but some individuals may initiate flowering in autumn or winter (Cubas 1999). In other parts of the world where it has been introduced and is considered an invasive weed (Lowe et al. 2000), it shows a great variation in flowering phenology. In the tropics, it flowers mainly in winter, as in Hawaii (Markin and Yoshioka 1996) or on Réunion Island (Indian Ocean) (Cadet 1974). In New Zealand, flowering occurs in autumn or spring, depending on the altitude (Hill et al. 1991). Finally, in South America, it flowers in spring or early summer. This ability to shift its flowering period in relation to local conditions may be one of the reasons for its ability to invade such a wide range of habitats. However, this often leads the species to flower at seasons when pollinators are scarce. In gorse native range, winter pollination should be challenging for the plants, and this is particularly the case in Brittany (west of France) and UK, where winter mean temperatures are below those considered necessary for pollinators' activity (bees and bumblebees). Gorses can provide nonetheless pollen as a food source for pollinators.

A detailed study performed on 16 natural populations of Brittany (France) has evidenced a within-population polymorphism for flowering phenology: long flowering individuals flower from autumn to spring and produce few flowers at a time, while short flowering individuals flower only in spring, and produce numerous flowers during a short period (Tarayre et al. 2007). Pods initiated in autumn or winter totally escape seed predation by the weevil *Exapion ulicis* (Coleoptera: Curculionidae), and the moth *Cydia succedana* (Lepidoptera), that infest, on average, 70% of the pods initiated in spring. The unusual flowering pattern of *U. europaeus* has thus

been interpreted as a bet hedging strategy, balancing the risks of seed predation in spring and unfavourable climatic conditions in winter (Tarayre et al. 2007).

Since *U. europaeus* has become invasive in many countries of the south hemisphere for more than a hundred years (Chater 1931), it is under continued study (Norambuena and Piper 2000; Ireson et al. 2003). The extended flowering period and the capacity of gorses to produce pods even during the unfavourable season can greatly enhance its invasive success. The weevil *E. ulicis* has been successfully introduced in several countries (Holloway and Huffaker 1957), but failed to efficiently control the spreading of *U. europaeus*, partly because gorse escape seed predation by flowering out of the reproductive season of the weevil (Hill et al. 1991). Thus, many studies are still performed on gorse biological control through herbivores and seed predators (e.g. Ireson et al. 2003), but these would be without a practical use if gorses are able to move their flowering period to less favourable season to escape the biological control agents.

A more complete assessment in its native range is still needed to understand, which factors influence flowering efficiency in the cold season. Indeed, the harsher conditions in winter should prevent or strongly reduce pollination and thus, reproductive success during this time of the year. In unfavourable climatic periods for pollinators, plants may insure their breeding either by promoting autonomous pollination through selfing, or by increasing flower longevity (Arroyo et al. 2006). As all Fabaceae, the gorses' anthers are located inside a keel, which requires the visit of an insect to open, therefore, the first hypothesis selfing seems unlikely although cleistogamic fertilisation cannot be excluded. The second hypothesis, increasing flower longevity, has not been tested.

The present study aims at clarifying how pollination, pod production and pod development can be efficient in winter. We want to know more specifically if pollination in the absence of insect visits can occur in *U. europaeus*. Moreover, we want to see if gorses invest more in reproductive structure in winter in order to compensate for the scarcity of winter pollinators, and the probable lower reproductive success due to the climatic conditions of the unfavourable season.

Material and methods

The biological model

Ulex europaeus is a perennial spiky shrub growing up to three meters tall and living up to 30 years. It is hexaploid, with $2n = 6X = 96$ chromosomes (Misset and Gourret 1996). In its native range, this plant is widespread along the Atlantic and the Channel coast, from Portugal to Scotland, and is highly common in Brittany (west of France), both along the coast and inland. It bears yellow hermaphrodite flowers made of an anterior keel, two lateral wings and a flag. Each flower bears 10 stamens and 12 ovules. Pollination is achieved by bees and bumblebees. The only reward is pollen, as the flowers do not produce any nectar. There is a polymorphism for flowering period, but we chose plants that were flowering from winter to spring, as we were interested here in the differences between seasons. The differences amongst plants of different flowering types are reported elsewhere (Tarayre et al. 2007). Polymorphism was found to have a genetic basis (Atlan et al. submitted), with plants individual ranking of flowering start remained constant through the years, while showing a plastic starting date depending of the climatic conditions of the year.

Exapion ulicis is a weevil seed predator specific to gorse (Holloway and Huffaker 1957). Females bore a hole in the pod wall with their rostrum (this takes 3–5 h), then lay their eggs inside the pod. Once hatched the larvae feed on the seeds. The adult weevils are released together with the seeds when ripe pods open. These weevils may attack up to 90% of ripe pods resulting from the spring flowering in England (Davies 1928), France (Tarayre et al. 2007) and New-Zealand (Hill et al. 1991), but are absent from pods resulting from autumn or winter flowering (Hill et al. 1991; Tarayre et al. 2007).

Measurement of floral traits

Measures were made on individuals from five natural populations (containing from 30 to more than 100 individuals), which are part of a longer term monitoring study (Atlan et al. submitted). These populations (La Réauté LR, Château de Vaux CV, Lande d'Oué LO, Ile Besnard IB, Pointe du Grouin PG) are located 5–70 km away from Rennes, and

represent typical gorse habitats in Brittany (heath land, fallow, field edge and seaside). All measurements were done in these five populations, but in two different years using six individuals per population for the pollen production in 2000–2001 and 10–12 individuals per population for the flower size in 2001–2002. Different individuals were used for the pollen production and the flower measurements.

Pollen per flower

We estimated pollen production from six plants per population in the five populations. Three flower buds ready to open per individual were collected at random across the individual in the morning. The same individuals were sampled twice, once in winter (December 2000) and once in spring (March 2001). The calice and corolla were removed and the buds were kept in individual Eppendorf tubes for at least 3 days to allow the anthers to open. The pollen was then extracted by centrifugation (5 min at 10,000 rpm). The pollen grains were counted, and their size estimated with an electronic particle counter (Coulter Counter Multisizer II (Beckman Coulter (UK) Ltd, High Wycombe, UK)). For each sample, we obtained the frequency distribution of pollen grain size. We observed a first small peak around 20 μm corresponding to non-viable pollen (devoid of cytoplasm), and a second large peak around 30 μm corresponding to viable pollen grains. Only fully viable pollen grains were taken into account.

Flower size

We estimated flower size from six individuals per population. Individuals were sampled once in winter (December 2001) and once in spring (March 2002). At each season, five open flowers per individual were collected at random across the individual. In total, we collected 300 flowers. Flowers were kept in 70% Ethanol and brought to the lab, where the total flower length and sepal length were measured using digital callipers.

Seed production and parasitism

We estimated the number of seeds per uninfested pod and the proportion of infested pods on mature pods

from 10 to 12 plants. Every two weeks from March until July 2001, we collected and opened 20–30 pods per individual. We estimated the number of seeds per uninfested pod with 8–10 pods devoid from parasites and did not count rotten or aborted seeds. According to Tarayre et al. (2007), pods reaching maturity from March to May were considered to result from winter flowering, and pods reaching maturity from June to July were considered to result from spring flowering. The winter estimate was the mean of values obtained from March to May and the spring estimate was the mean of the values obtained from June to July.

Monitoring of bagged flowers

Three plants were chosen in the population closest to Rennes (Château de Vaux), and four shoots per plant were enclosed in a bag of tulle after the removal of all pods, open or faded flowers. Two bagged shoots were kept untouched, to test whether pollination was possible in the absence of insects, and the two others were hand-pollinated, to ensure that bagging did not prevent pod formation. This was done once in November 2000 and once in March 2001, thus, we had a total of 24 bagged shoots for all experiments. Each shoot produced 5–20 new flowers, for a total of about 140 flowers for the winter cohort and 200 flowers for the spring cohort across the three plants.

Monitoring of individual flowers

To monitor individual flowers, we used 10 individuals located on the campus of the University of Rennes 1, in Brittany (western France). They were chosen close to the laboratory to facilitate the daily

visit needed to have precise phenological data on each individual flower. This population is 5–70 km away from the five other populations of the study and present slightly more favourable conditions, as the proximity of the town can increase the average temperature. Nevertheless, flowering periods were similar to other populations in Brittany.

This monitoring was performed from January until June 2002. To estimate the precise chronology of flowering from bud to mature pod, we performed a daily visit during the flowering period and a weekly visit during pod maturation. We had an observation period in winter and another one in spring. We monitored 36 flowers from buds open in January (six flowers per individual for four individuals and 12 flowers for one individual) and 50 flowers from buds open in April (five flowers per individual for 10 individuals).

Statistical analyses

The statistical analyses were performed with SAS (SAS 2005) using the PROC GLM (type III) for ANOVAs and the PROC CORR for Pearson correlations. In the ANOVA model, population (chosen to represent different gorse habitats) and season (our treatment) were fixed factors, and individuals were nested within population. Proportions were compared by a χ^2 test. We controlled experiment-wise type 1 error with the Bonferroni correction.

Results

Measurement of floral traits

All variables measured depended on the individual, but not on the population of origin (Table 1). Pollen

Table 1 Analyses of variance on floral traits and seed production measures on *Ulex europaeus* in Brittany

| Source | Pollen quantity $N = 121$ | | | Pollen size $N = 121$ | | | Petal length $N = 196$ | | | Sepal length $N = 196$ | | | Seeds per pod $N = 88$ | | |
|--------------|---------------------------|------|--------|-----------------------|--------|--------|------------------------|------|--------|------------------------|------|--------|------------------------|------|------|
| | Df | F | P | Df | F | P | Df | F | P | Df | F | P | Df | F | P |
| Population | 4 | 2.62 | 0.06 | 4 | 0.37 | 0.82 | 4 | 1.80 | 0.17 | 4 | 1.79 | 0.17 | 4 | 1.69 | 0.17 |
| Ind (pop) | 20 | 3.82 | <0.001 | 20 | 5.95 | <0.001 | 21 | 9.14 | <0.001 | 21 | 2.77 | <0.001 | 53 | 2.18 | 0.02 |
| Season | 1 | 1.69 | 0.20 | 1 | 181.39 | <0.001 | 1 | 0.22 | 0.63 | 1 | 1.76 | 0.18 | 1 | 1.07 | 0.31 |
| Pop × Season | 3 | 1.81 | 0.15 | 3 | 2.09 | 0.11 | 3 | 5.97 | <0.001 | 3 | 1.75 | 0.16 | 4 | 2.42 | 0.07 |

N indicates the sample size. Population and Season are fixed factors. Ind (pop): individuals nested within populations. Alpha is set at 0.0025

production differed little between winter and spring either for mean quantity ($23,290 \pm 850$ vs. $22,015 \pm 828$ pollen grains per flower on average (\pm standard error) or size ($30.6 \pm 0.14 \mu\text{m}$ vs. $32.9 \pm 0.14 \mu\text{m}$ on average), although the difference is significant for the latter (Fig. 1, Table 1). Pollen quantity and size were positively and significantly correlated ($R^2 = 0.149$, $N = 199$, $P < 0.0001$). Measures made on flower size also showed comparable

mean values in winter and spring for both petal length (15.38 ± 1.39 vs. 16.19 ± 1.74 cm on average) and sepal length (12.35 ± 1.09 vs. 13.31 ± 1.25 cm on average) (Fig. 1). The significant population \times season interaction indicates that three populations (CV, LR, PG) out of the five showed a significant difference for higher petal length in spring compare to winter, while the two other populations presented the same trend. The differences are of 5%. Petal and sepal lengths were positively and significantly correlated ($R^2 = 0.619$, $N = 294$, $P < 0.0001$). Pods resulting from winter flowering contained slightly more seeds than pods resulting from spring flowering (4.20 ± 0.24 vs. 3.59 ± 0.13 seeds per pod on average), but this difference was not significant (Table 1).

Overall, the differences found between winter and spring for pollen production, flower size and seed production are small and statistically significant only for pollen size, with larger pollen grain in spring compared to winter.

Monitoring of bagged flowers

Flowers enclosed within bags and hand-pollinated did produce pods in all plants and in both seasons (63 pods in total), showing that bagging *per se* did not prevent pod formation. Flowers enclosed within bags and not hand-pollinated did not produce any pods in any plants showing that fertilisation was impossible in the absence of pollen vectors. In addition, keels of non-pollinated flowers stayed closed until the fading of the flowers, indicating that an open keel can be considered reliable evidence for an insect visit.

Monitoring of individual flower

The detailed monitoring made on the Campus of Rennes in 2002 gave us information on the flowering and fruiting processes depending on the season. Out of the 86 flowers marked, eight were lost at various times and thus not counted. Due to additional missing observations, only 70 winter flowers and 68 spring flowers were used for time to pollination and time to wilting. Pollinators (bees and bumblebees) were observed all year long. Bumblebees belonged to the genus *Bombus* (mainly *Bombus terrestris*), and bees belonged either to *Apis* or to *Anthophora* genera. They

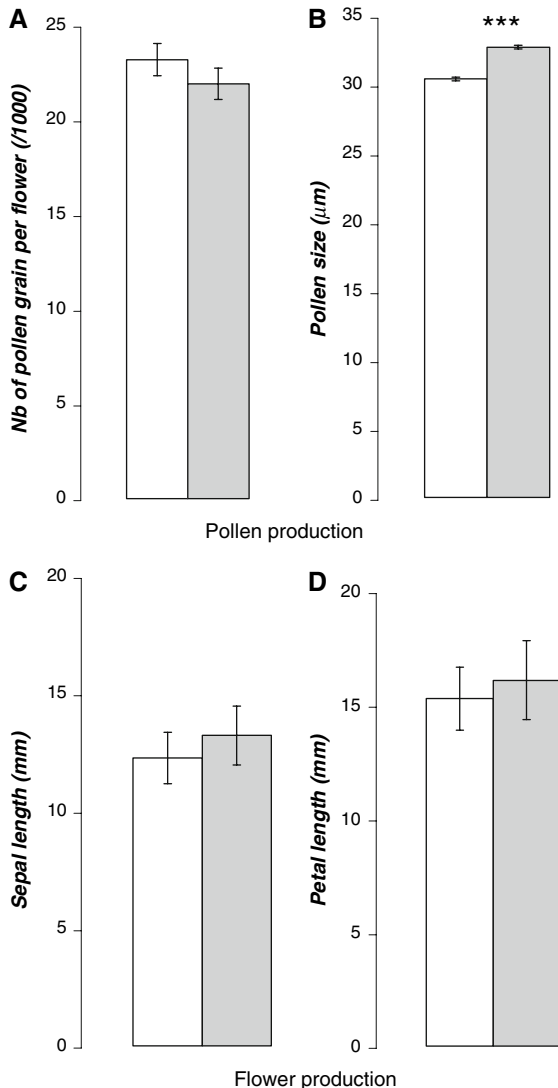


Fig. 1 Pollen and flower measurements of *Ulex europaeus*. Pollen quantity (a), pollen size (b), sepal length (c) and petal length (d) of winter (white columns) and spring (filled columns) flowers. Columns show mean values of five natural populations and bars denote associated standard error. *** $P < 0.001$

were observed frequently in spring, and more rarely in winter when they were only active in the middle of the warmer sunny days. In the coldest months (January and February), the most frequent pollinators were *Apis mellifera*, which we observed repeatedly for the three following years (Anne Atlan, personal communication).

Flowers with an open keel were considered as having been insect pollinated. On average, flowers opening in January were pollinated after 2 ± 0.4 days, and faded after 21 ± 1.7 days, while flowers opening in April were pollinated after 12 ± 5 h, and faded after 9 ± 0.3 days (Fig. 2). Both differences are significant ($N = 70$, $F = 16.67$, $P < 0.0001$ and $N = 68$, $F = 104.79$, $P < 0.0001$ respectively). All the 86 flowers were pollinated whatever the season and the rate of flower abortion was extremely low in winter and spring (Table 2).

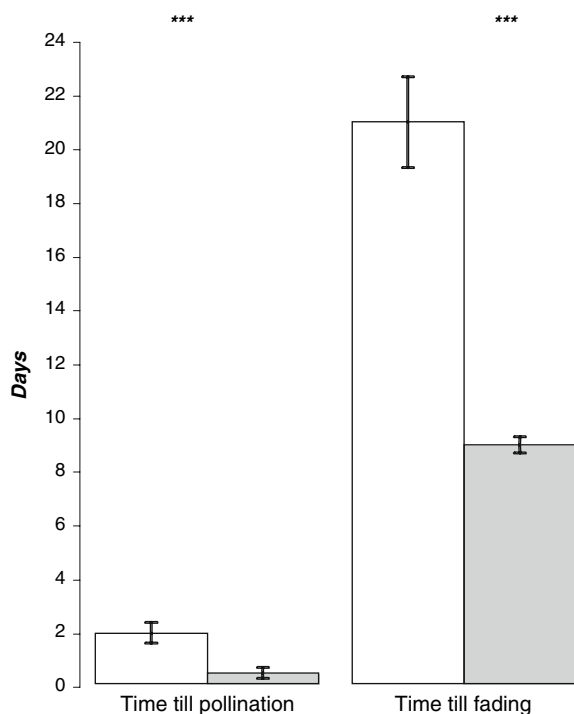


Fig. 2 Phenology of individual flowers of *Ulex europaeus* monitored on the Campus of Rennes (France). Winter values (white columns) come from flowers open in January. Spring values (filled columns) come from flowers open in April. Columns show mean values of 70 flowers and bars denote associated standard error. Significance was tested with a one-way ANOVA. *** $P < 0.001$

Pod development was slower in winter than in spring: pod maturation took on average 121 ± 2.5 days from pollination to dehiscence for the winter cohort and 83 ± 1.3 days for the spring cohort ($N = 51$, $F = 224.5$, $P < 0.001$). The rate of pod abortion was non-significantly higher in winter (53%) than in spring (27%) after Bonferroni corrections (Rice 1989). The causes of abortion were not distinguished (Table 2). Most pod abortion occurred during the first 70 days in winter and the first 20 days in spring.

Seed production was recorded for only 14 pods in winter and 28 pods in spring because the others opened before observation. The pods were spread across the 10 individuals of the study. None of the winter pods was attacked by seed predators and, in fact, winter pods produced an average of 3.07 ± 0.6 seeds per pod. For the 28 spring pods, 19 were infested by *E. ulicis*, and the uninfested pods produced an average of 2.93 ± 0.5 seeds per pod.

Discussion

The pollination rate was very high both in winter and in spring, since all the flowers monitored in the Rennes Campus in 2002 were pollinated. A set of 16 natural populations monitored in the same year in Brittany showed comparable pod and seed productions from winter and spring flowers (Tarayre et al. 2007). However, during the monitoring of five populations performed from 2000 to 2006 (Atlan et al. submitted), pollination deficit was observed in populations located on forest hedges and during the coldest winter (2003). Such spatio-temporal variation in pollinator visitation rates is common (Horvitz and Schemske 1990; Parker 1997; Herrera 1989), but despite these variations, the potential of pollination of winter flowers of *U. europaeus* in Brittany is high. Since *U. europaeus* could not be pollinated in absence of pollen vectors (bagged flowers), such a high pollination success implies efficient insect pollination even during the cold season.

Availability of pollinating insects

The main pollinators of gorse are bees and bumblebees, two insects that need relatively warm

Table 2 Phenology of individual flowers of *Ulex europaeus* monitored on the Campus of Rennes (Brittany)

| | Winter | Spring | <i>N</i> | <i>F</i> | χ^2 | <i>P</i> |
|---|------------|-------------|----------|----------|----------|----------|
| Mean time before pollination (in days) | 2 ± 0.4 | 0.5 ± 0.2 | 84 | 16.67 | – | <0.0001 |
| Mean time before fading (in days) | 21 ± 1.7 | 9 ± 0.3 | 84 | 104.79 | – | <0.0001 |
| Mean time before pod abortion (in days) | 82.6 ± 7.7 | 28.2 ± 21.6 | 47 | 142.8 | – | <0.0001 |
| Mean duration of pod ripening (in days) | 121 ± 2.5 | 83 ± 1.3 | 51 | 224.5 | – | <0.0001 |
| Proportion of flower abortion | 0.03 | 0.02 | 86 | – | 0.05 | NS |
| Proportion of flower pollination | 1 | 1 | 84 | – | 0 | NS |
| Proportion of pod abortion | 0.53 | 0.27 | 79 | – | 5.79 | NS |
| Proportion of flowers producing ripe pods | 0.43 | 0.72 | 81 | – | 7.94 | <0.005 |
| Proportion of infested pods | 0 | 0.68 | 42 | – | 20.28 | <0.0001 |

Winter values come from flowers open in January. Spring values come from flowers open in April. For time values, means are given ± standard deviance. Significance was tested with one-way ANOVA for the time values and χ^2 for proportions. Alpha is set at 0.0056

temperature to be active (above 11°C for bees, and 6°C for bumblebees, which are able to warm-up by muscle contraction, Heinrich 1979). However, to our knowledge, no studies investigated the foraging behaviour of these species in winter. In Rennes, where the flower monitoring was performed, the mean (±SD) monthly temperature measured between 1971 and 2003 is 5.45 ± 2.16°C in January (7.4°C in 2002) and 9.75 ± 1.15°C in April (10.2°C in 2002) (Ferren 2004). The year of observations was, therefore, warmer than the mean of the past 33 years, but lay within the usual range of temperature of this region. These official temperatures are always measured in the shade, while temperature in the sun may be up to 8°C higher. However, bumblebees hibernate during the coldest months, and the main pollinator in January appeared to be *Apis mellifera*. It is indeed well known by bee keepers that the proximity of gorse populations advances and increases honey production, both in France (personal observation) and in New Zealand (Hill and Sandrey 1986). Temperature above 11°C occurs almost daily in spring, but is achieved in winter only in the middle of the warmest sunny days. Although we did not measure the temperature in our field populations, we did observe bees actively foraging only on favourable days in winter. The daily probability of being visited is, thus, much lower in winter than in spring. This difference seems to be compensated by the opening duration of flowers: flowers stayed open twice as long in winter than in spring. They opened for so long in winter (21 days) that they had a high probability to be open and receptive when a

favourable day occurred. This difference may result from developmental constraints and/or from selection. Indeed, low temperature may conserve the flower opening for a longer period for metabolic reasons as in roses (Monteiro et al. 2001). Such constraints can, however, hardly explain a doubling of flower longevity, and the selective hypothesis seems more likely. Several authors (Arroyo et al. 2006; Ashman and Schoen 1994; Neiland and Wilcock 1995; Osada and Sugiura 2006; Van Doorn 1997; Zhang et al. 2006) found that higher flower longevity was advantageous when pollinators were not reliable. Arroyo et al. (2006) have coined this phenomenon “increased pollination probability hypothesis”. In *Aconitum gymnanthum*, increased flowering longevity in high altitude populations compared to lower altitude populations resulted in enhanced pollination success (Zhang et al. 2006). Also, Osada and Sugiura (2006) compared an early flowering species, *Pieris japonica*, and a late flowering species, *Lyonia ovalifolia*, both from the same family and habitat, and both pollinated by bumblebees. The first species compensated the rarity of pollinators early in the season by a longer flowering duration.

Attractiveness of flower to pollinators

A high rate of pollination requires not only the presence of pollinators, but also attractive and efficient flowers. Here we have tested two of the traits linked with flower attractiveness, flower size

(Caruso 2000) and pollen production (Faegri and van der Pijl 1971). Indeed, pollen is used by bees to feed their larvae, and may even be a more important reward than nectar for bumblebees (Cresswell and Robertson 1994; Passarelli and Bruzzone 2004). Thus, keeping pollen production high in winter maintains its attractiveness to bees and bumblebees, and insures efficient pollination. Our results show that both petal and sepal were of comparable size in winter and spring, and that pollen production was as numerous in winter as in spring. In both seasons, a flower produced around 20,000 pollen grains, which is the range expected for insect-pollinated species where the only reward is pollen (Faegri and van der Pijl 1971). The only variable showing significant seasonal differences is pollen size, that is slightly lower in winter than in spring, but this decrease in size is only of 5%, hardly reducing flower attractiveness. Furthermore, *U. europaeus* is almost the only plant flowering in Brittany during winter (Des Abbayes et al. 1971), thus reducing competition with other species for the rare pollinators present. In addition, winter flowering individuals of gorse are a minority and produce few flowers at a time (Tarayre et al. 2007), so that even within species, competition is also lower in winter.

Flower and pod development

The most important difference between winter and spring in the development from bud to mature pod is the 21 days long winter flower opening, which insures that pollination is not limiting even in less favourable climatic conditions. Pods developed more slowly in winter and were more prone to abortion than in spring, perhaps because the number of flowering plants is low, which increases the probability of selfing and subsequent inbreeding depression. Indeed, across all populations studied, only 20% of plants on average exhibit the long flowering phenotypes, the others flower only in spring (Tarayre et al. 2007). Pods may also abort due to frost, but this situation was not observed in 2002, where winter was mild and pods did not freeze, so that 43% of winter flowers produced ripe pods. In addition, the winter cohort of pods was totally devoid of seed predators, while the spring cohort suffers a high rate of infestation by the weevil *Exapion ulicis*.

The number of seeds per uninfested pod was slightly higher in the winter pods compared to the uninfested spring pods, which may result from the preference of *E. ulicis* for pods with the highest number of seeds (Barat et al. 2007). All this suggests that the winter seed production of long flowering plants is higher than their spring seed production and this is accordance to other studies (Atlan et al. submitted).

A trade-off between winter and spring production is also possible. Indeed, the use of resources from the plants necessary to produce pods and seeds is certainly limited. Plants heavily flowering already in winter would not have enough resources to produce many pods in spring, while plants flowering in spring only can invest all their resources in the pod production at once.

Reproduction showing bet hedging depending on the climate

The winter flowering of gorse is unusual for an insect pollinated plant under the seasonal climate of Europe. This feature is considered as a way to escape seed predation (Tarayre et al. 2007), a strategy described by Janzen (1971) and supported by various examples, although most of them are in tropical climates (Derr 1980; Carroll and Loyer 1987). However, under temperate conditions, escaping parasitism in time may also be successful, as for the Fabaceae, *Astragalus utahensis* (Green and Palmbald 1975), but a trade-off is often observed between pollination and avoidance of parasitism. For example, the Ericaceae, *Vaccinium hirtum* (Mahoro 2002) flowers in spring and faces a dilemma: plants flowering early suffered a lack of pollinators, while plants flowering late were more heavily attacked by weevils and flies. One can expect an integrated response from the plant balancing constraints imposed by pollinators, herbivory and climate (Brody 1997; Elzinga et al. 2007). In *U. europaeus*, the constraints from pollinators in winter might be reduced by the longevity and the attractive display of the winter flowers, thus reducing selection pressure from lack of pollinator in winter, while the pressure exerted by the seed predators in spring is quite high. Thus, flowering at two different seasons can be selected as bet hedging strategy to cope with these antagonistic selective pressures (Bolmgren et al. 2003), as is the case, for example,

for the long flowering herb *Lobularia maritime* (Pico and Retana 2001). In addition, the high potential pollination of gorse winter flowers gives it a high adaptive potential. This could also lead to disruptive selection, as plants flowering only in Spring would be selected to increase their pod production or their defences against the seed eater, while the plants starting flowering in winter should shift their all production in winter and produce some cold resistance mechanisms to optimise pod survival in winter.

In other continents where *U. europaeus* has become invasive for 100 years, the flowering phenology has shifted heavily towards the unfavourable season, and has thus escaped from most seed eating biocontrol agent that have been introduced. Similarly to Europe, the insects do not attack pods produced in the unfavourable season and have shown no capacities yet to shift their phenology to match their host.

More generally, we can relate efficient seed production under a large range of climate to an increase of invasion capacity. High seed production, early flowering and high phenotypic plasticity are part of the “ideal weed” characteristics described by Baker (1974) and play a role in the new cosmopolitan distribution of *Ulex europaeus*.

Acknowledgements We are grateful to Olivier Villas, Ellen Lamborn for their help in pollen counting, and to Mark Macnair for receiving us in its lab (University of Exeter, UK). We thank Heinz Müller-Schärer, Luc Gigord and two anonymous reviewers for useful comments on the manuscript.

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